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Effect of *Prosopis* (mesquite) invasion and clearing on vegetation cover in semi-arid Nama Karoo rangeland, South Africa

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The Nama-Karoo is the largest of the three biomes that comprise the semi-arid Karoo-Namib ecoregion of southern Africa. Large tracts of Nama-Karoo rangeland have been invaded by alien leguminous trees of the genus *Prosopis*. We assessed the impact of *Prosopis* invasion and clearing on vegetation cover in heavily grazed Nama-Karoo rangeland on two sheep farms in the Beaufort West district of the Western Cape province of South Africa. Our results suggest that, below critical threshold cover levels, *Prosopis* trees do not affect indigenous vegetation and add to overall rangeland vegetation cover. However, once *Prosopis* cover exceeds critical thresholds, the trees begin to negatively impact on indigenous vegetation (especially grasses) and overall vegetation cover. In addition, our data suggest that vegetation cover recovers after *Prosopis* clearing, being temporarily higher than pre-invasion levels possibly as a result of enhanced post-invasion soil fertility. Lastly, our results suggest that *Prosopis* trees reduce rangeland erosion potential at low cover and increase it after they exceed critical threshold cover. Information about thresholds of *Prosopis* impact can be used to direct clearing efforts for maximum benefit when resources are limited.

Keywords: invasive plants – exotic, Nama Karoo, rehabilitation, semi-arid, soil erosion

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Introduction

Land degradation caused by soil erosion is one of the most critical environmental issues affecting South Africa (Le Roux et al. 2007, 2008). More than 70% (>854 000 km^2) of South Africa's land surface has been affected, to varying intensities, by soil erosion (Le Roux et al. 2008). Much of the erosion in these areas has been facilitated by a combination of highly erodible soils and poor farming practices (Le Roux et al. 2007).

In South Africa's semi-arid region, extensive overgrazing has led to widespread soil erosion and drying up of rivers and rangeland (Milton and Dean 1995). The concomitant spread of invasive alien plants (IAPs) across the region (Milton et al. 2003) could have intensified soil erosion by enhancing deleterious effects of over-grazing on rangeland vegetation cover. Vegetation cover is an important determinant of rainfall infiltration, runoff and ultimately soil erosion potential (Elwell and Stocking 1976; Dunne et al. 1991; Le Roux et al. 2008; Zuazo and Pleguezuelo 2008). Plant canopy cover (i.e. the proportion of the ground surface covered by aerial plant parts) promotes infiltration and limits runoff by protecting the soil surface from raindrop impact, which causes detachment of soil particles and physical crusting (Elwell and Stocking 1976; Herrick et al. 2005a). Plant basal cover (i.e. proportion of the soil surface covered by plant bases) reduces the erosive ability of runoff by dissipating its power through deflection and obstruction (Rogers and Schumm 1991; Herrick et al. 2005a).

The Nama-Karoo is the largest of the three biomes that comprise the semi-arid Karoo-Namib ecoregion of southern Africa (Palmer and Hoffman 1997). In South Africa, the biome occupies ~346 100 km^2 (28% of the country) and supports extensive commercial sheep and goat production on natural rangeland (Palmer and Hoffman 1997; Hoffman 1999; Suttie et al. 2005). Large areas of the Nama-Karoo have been invaded by an array of IAPs (Richardson and van Wilgen 2004; Henderson 2007). Notable among the IAPs are leguminous trees of the genus *Prosopis*, which cover at least 18 000 km^2 of the biome's low-lying alluvial plains and seasonal watercourses (Richardson and van Wilgen 2004). *Prosopis* trees, which are indigenous to the Americas, were introduced into arid regions of South Africa in the late 1880s to provide shade, fodder and fuel wood (Zimmermann and Pasiecznik 2005). However, alien *Prosopis* trees have had serious negative impacts on the environment and human livelihoods (Richardson et al. 2000; Richardson and van Wilgen 2004; Zimmermann and

Pasiecznik 2005; Ndhlovu et al. 2011; Dzikiti et al. 2013; Schachtschneider and February 2013; Shackleton et al. 2015b, 2015c). In many areas, the trees have coalesced to form dense thorn thickets that are thought to have displaced and suppressed indigenous vegetation (Richardson et al. 2000; Richardson and van Wilgen 2004). There is, however, no information on how *Prosopis* invasion in Nama-Karoo rangeland may have affected vegetation cover and consequently soil erosion potential. The effect of vegetation cover on soil erosion potential is especially significant in semi-arid areas such as the Nama-Karoo where seasonal and annual drought cycles limit the development of vegetation (Smith et al. 1962). Likewise, the impact of invading alien trees on vegetation cover is likely to be significant in naturally treeless ecosystems (Rundel et al. 2014) such as the Nama-Karoo.

Extensive areas of the Nama-Karoo have been cleared of *Prosopis* under a government-led IAP control programme (Zimmermann and Pasiecznik 2005). The programme, called Working for Water (WfW), is principally aimed at securing threatened water resources by clearing IAPs from South Africa's major watersheds (Le Maitre et al. 2000, 2002; Zimmermann and Pasiecznik 2005). Most of the clearings have been carried out using the standard WfW practice of reducing the aboveground biomass of alien plants and leaving the indigenous vegetation to recover without further intervention (Blanchard and Holmes 2008; Reinecke et al. 2008). In addition to securing water resources, there is a widely held expectation that WfW clearings will lead to restoration of other ecosystem functions, such as soil cover and erosion control.

Numerous savanna bush encroachment and tree thinning studies in South Africa have shown that increases in woody plant abundance invariably suppress herbaceous plants while removal of all or some of the trees promotes herbaceous growth (Smit and Rethman 1999; Smit 2003, 2005). The relationship, however, is complicated by the interplay of antagonistic negative and positive tree–herbaceous plant interactions at the individual tree neighbourhood and subcanopy level (Smit 2005). The abundance of herbaceous plants under and near tree canopies may be enhanced by the favourable microclimatic and nutrient conditions that occur there, while at the same time being suppressed by low irradiance and competition for other more limiting belowground resources (Scholes and Archer 1997). The net result of the positive and negative tree–herbaceous plant interactions usually depends on the tree's size/age and on tree density at the landscape level (Scholes and Archer 1997; Smit 2005). Facilitation processes are usually more effective than competition under and near small young trees, enhancing herbaceous production; however, as trees and shrubs become larger, competitive processes usually overshadow facilitation and adversely affect herbaceous production (Scholes and Archer 1997; Riginos et al. 2009). The positive effects of trees on herbaceous diversity and production are usually greater where there are a few trees than where there are no trees, but the trend is reversed at high tree densities (Scholes and Archer 1997; Riginos et al. 2009).

As a result of the antagonistic tree–herbaceous interactions outlined above, herbaceous plant abundance in semi-arid savanna does not decline in a simple way with increasing woody plant abundance during 'bush encroachment' but is stable up to a certain critical level after which it begins to decrease with increasing tree density (Scholes and Archer 1997; Smit 2005). Given that herbaceous plants provide most of the vegetation cover in many semi-arid rangelands (Herrick et al. 2005a), such threshold effects could also apply to the relationship between *Prosopis* and indigenous vegetation cover in Nama-Karoo rangeland. Thresholds have been reported for *Prosopis* effects on grazing capacity in Nama-Karoo rangeland (Ndhlovu et al. 2011) and herbaceous forage production in arid and semi-arid rangelands in the South and Southwestern United States (McDaniel et al. 1982; Warren et al. 1996).

We assessed the effects of *Prosopis* invasion and clearing on vegetation cover in heavily grazed Nama-Karoo rangeland on two sheep farms near the town of Beaufort West in the Western Cape province of South Africa. Our aims were to (1) determine the effects of invasion and clearing on rangeland vegetation cover (plant canopy and basal cover), and (2) identify the vegetation changes that underlay the effects. Based on information from savanna bush encroachment and tree thinning studies, we hypothesised that (1) *Prosopis* invasion would reduce overall vegetation cover in Nama-Karoo rangeland, while (2) clearing would lead to recovery of pre-invasion levels. In addition, we expected (3) the effects of *Prosopis* invasion on overall canopy and basal cover to intensify as invasions became denser, demonstrating a threshold effect in which *Prosopis* trees only begin to impact on the canopy and basal cover of indigenous plants after they surpass a certain cover. Lastly, we expected (4) the changes in overall rangeland vegetation cover to be closely linked to changes in grass cover. *Prosopis* trees are known to especially reduce grass abundance in their understory and neighbourhood (McDaniel et al. 1982; McClaran and Angell 2006; Simmons et al. 2008).

Materials and methods

We used the generic term *Prosopis* because of the uncertainty surrounding *Prosopis* classification to species level in South Africa. A number of naturalised *Prosopis* species have hybridised extensively such that most populations in South Africa are composed of overlapping morphotypes that are difficult to classify into distinct species (Zimmermann 1991; Roberts 2006; Zachariades et al. 2011; Mazibuko 2012). Many South African studies have not attempted to classify *Prosopis* populations further than the general terms *Prosopis* or mesquite.

Study site

Our study was conducted on the farms 'De Hoop' (32°10′13″ S, 22°47′5″ E) and 'Brandwag' (32°11′36″ S, 22°48′19″ E), located about 30 km north-east of the town of Beaufort West in the Western Cape province of South Africa (Figure 1). At the time of our study (June and October 2009), De Hoop farm was covered by stands of invasive *Prosopis* trees while the neighbouring Brandwag farm had been completely cleared of *Prosopis* by WfW teams between 2003 and 2005. *Prosopis* clearing consisted of

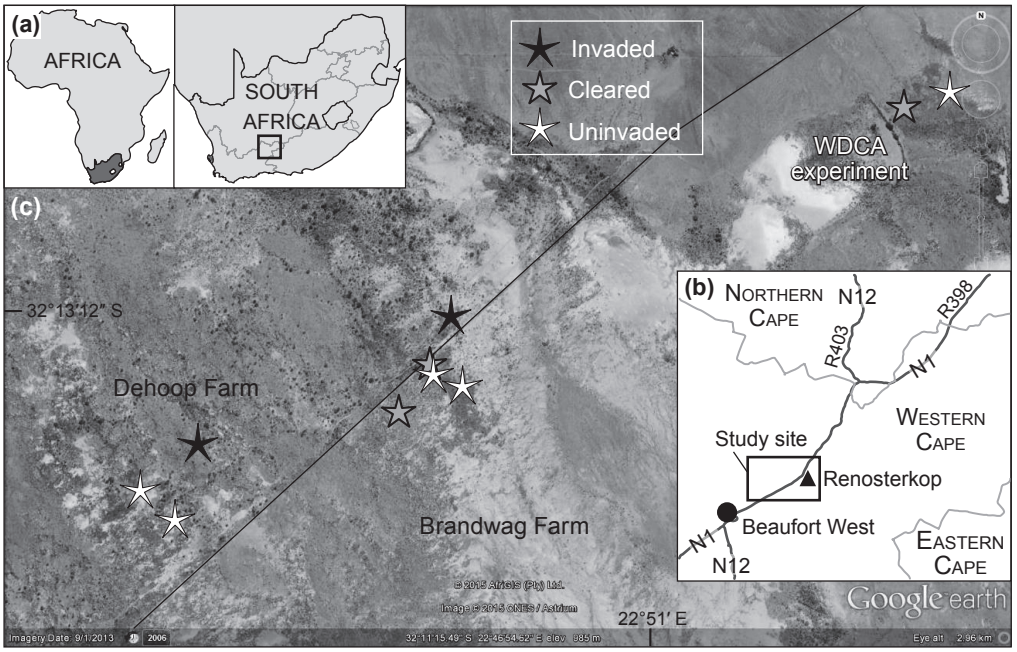

Figure 1: Map showing the location of the study site (a, b) and the placement of sampling plots (c). Satellite image obtained from Google Earth

felling trees at 100 mm above ground level and treating stumps with Garlon® 4 herbicide (triclopyr ester) at a 4% dilution with diesel. Felled wood and branches were left lying in the field and no further interventions were taken to aid the recovery of indigenous vegetation. The farms were stocked with sheep and the vegetation showed signs of severe overgrazing.

The natural vegetation on De Hoop and Brandwag is mainly Gamka Karoo with small areas of Southern Karoo Riviere and Upper Karoo Hardeveld (Mucina and Rutherford 2006). Gamka Karoo vegetation is characteristically dominated by dwarf shrub genera in the families Aizoaceae (*Drosanthemum* and *Ruschia*) and Asteraceae (*Eriocephalus*, *Pentzia* and *Pteronia)* interspersed with grasses (*Aristida*, *Enneapogon*, *Digitaria* and *Stipagrostis)* (Palmer and Hoffman 1997). Taller shrubs and trees (*Vachellia karroo* (Hayne) Banfi & Galasso [*Acacia karroo* Hayne], *Euclea undulata* Thunb. and *Rhigozum obovatum* Burch.) occur intermittently (Palmer and Hoffman 1997).

The soils are minimally developed lithosols over mudstones. The study was located on a gently sloping alluvial plain traversed by dry river courses and flanked on the west and north by an extensive plateau. The area experiences highly seasonal rainfall with unimodal peaks occurring from December to March (Palmer and Hoffman 1997). Mean annual rainfall is 239 mm (Kraaij and Milton 2006) but annual rainfall had, however, been generally higher than the long-term average during the eight years preceding the study (2000–2008; South African Weather Service unpublished data).

Sampling and data collection

We identified sites within Brandwag and De Hoop that were invaded (n = 5), cleared (n = 3) and uninvaded (n = 5) by *Prosopis* (Figure 1). All cleared sites were located in Brandwag while invaded sites were restricted to De Hoop. Cleared sites included areas cleared in 2003, 2004 and 2005. Uninvaded sites were located in both Brandwag and De Hoop. Sampling sites were selected to be as environmentally similar (topography, soil type, on Gamka Karoo vegetation, etc.) as possible. Invaded and cleared sites had comparable *Prosopis* tree size class distributions (determined from basal diameters of standing trees in invaded sites and tree stumps in cleared sites). Invaded sites had an average *Prosopis* canopy cover of approximately 15%. Since it was difficult to determine the precise years when clearing occurred at cleared sites, clearing impacts were conservatively interpreted as relating to conditions 4–6 years after *Prosopis* clearing.

Line-point intercepts were used to measure the proportion of the soil surface that was covered by plants (Herrick et al. 2005a). Line point intercepts were visually extended upwards to estimate *Prosopis* canopy cover. In each plot, five 100-metre transects were laid out at 10-metre intervals along a 50-metre east–west trending base line. Two 50-point line-point intercept readings were made along each 100-metre transect using 50-metre tape. A total of 50, 20 and 30 50-metre line-point intercepts were set up on uninvaded, invaded and cleared sites, respectively.

Data analysis

Plant canopy and basal cover

Plant canopy cover referred to the proportion of the ground surface covered by plant parts (leaf, stem, etc.; Herrick et al. 2005a). Only the uppermost plant species were considered part of plant canopy cover, while species occurring in lower layers were ignored (Herrick et al. 2005a). Percent canopy cover per transect was calculated by dividing the number of plant canopy intercepts by 50 and multiplying by 100 (Herrick et al. 2005a). Basal cover referred to the proportion

of the soil surface that was covered by plant bases (Herrick et al. 2005a). Percent basal cover per transect was calculated in the same manner as canopy cover. Overall plant canopy and basal cover included *Prosopis*.

Species and functional type canopy and basal cover
Species canopy/basal covers per transect were determined by dividing the number of individual species canopy/basal intercepts by 50 and multiplying by 100. Plant functional type (annual grass, perennial grass, annual herb, perennial herb, succulent shrub, non-succulent shrub and tree) canopy/basal covers per transect were calculated by summing the canopy covers of species falling within each of the functional groups. Species were classified into functional types using published descriptions (Meredith 1955; Le Roux et al. 1994; Shearing and van Heerden 1994; Esler et al. 2006).

Statistical analyses

Effect of Prosopis *invasion and clearing on rangeland vegetation cover*
The effect of *Prosopis* invasion and clearing on rangeland vegetation cover was evaluated by comparing mean overall plant canopy and basal cover in uninvaded, invaded and cleared plots. Differences between uninvaded vs invaded, invaded vs cleared and uninvaded vs cleared plots were taken to represent the impacts of invasion and clearing. Likewise, the vegetation dynamics that underlay overall plant canopy and basal cover changes following invasion and clearing were deduced from differences in mean plant species and functional type canopy and basal covers between the plots. In order to focus our analysis on the most important vegetation dynamics, only plant functional types whose mean canopy and basal covers differed significantly between the plots were analysed to species level. The relative importance of the vegetation changes were evaluated by considering the magnitude of the differences in mean plant functional and species canopy and basal cover values between plots.

Means and standard errors were calculated using the Paleontological Statistics Software Package for Education and Data Analysis (PAST; Hammer et al. 2001). Significance was assessed by one-way analysis of variance via randomisation (10 000 randomisations) using the software Resampling Procedures 1.3 (David C Howel, University of Vermont; available at http://www.uvm.edu/dhowell/statPages/Resampling/Resampling.html). Differences were considered significant at $p \leq 0.05$. Non-parametric randomisation (Manly 1997) was used because the data was non-normal. Normality was tested using the Shapiro–Wilk test (Shapiro and Wilk 1965). Adjustments for multiple comparisons were made using a false discovery rate (FDR) based procedure (two-stage sharpened method, maximum acceptable FDR = 0.05) (Pike 2011). The FDR-based adjustments were conducted using the spreadsheet provided with the online version of Pike (2011). Adjustments for multiple comparisons in large bodies of data are required in order to avoid rejecting null hypotheses too readily (type 1 error) (Curran-Everett 2000). A number of statistical methods have been developed to control for type 1 error in multiple comparisons (Pike 2011). FDR-based methods are currently considered to be the most suitable for ecological data (Curran-Everett 2000; García 2004; Pike 2011).

Effect of increasing invasion density on plant canopy and basal cover
The effect of increasing invasion density on overall plant canopy and basal cover was determined from the relationship between increasing *Prosopis* cover and overall plant canopy and basal cover. These relationships were assessed by segmented (piecewise) linear regression using *Prosopis* and overall canopy and basal covers derived from transects set up in invaded sites. The regressions were conducted using the program SegReg (RJ Oosterbaan, International Institute for Land Reclamation and Improvement; available at http://www.waterlog.info/segreg.htm). Segmented regression applies linear regressions to data that do not have strong linear relations by introducing one or more breakpoints (Oosterbaan 1994). Separate linear regressions are then performed for the separate linear segments. SegReg selects, based on significance and maximal explanation of variation, the best-fitting breakpoint and linear regressions from seven predefined functions (Oosterbaan 2005). The models are configured as follows: Type 0 is a single horizontal line without a breakpoint (no relationship), Type 1 is a single sloping line without breakpoint (linear regression), Type 2 is a succession of two connected segments with sloping lines, Type 3 is a horizontal segment followed by a sloping line, Type 4 is a sloping segment followed by a horizontal line, Type 5 is a step function with two horizontal segments with significantly different means and Type 6 consists of two disconnected segments with sloping lines (Oosterbaan 1994, 2005).

Results

Effect of invasion and clearing on plant canopy cover

Invasion did not reduce overall plant canopy cover, whereas clearing increased it from 42% to 76% (Figure 2). Overall plant canopy cover in cleared rangeland was still 40% higher than the pre-invasion level more than four years after clearing (Figure 2). Overall mean plant canopy cover did not differ significantly ($F = 0.43$, $P = 0.563$) between uninvaded (45.35 ± 2.50%) and invaded (42.00 ± 4.05%) sites. Cleared sites had significantly higher ($F = 37.92$, $P < 0.001$) overall mean plant canopy cover (76.31 ± 3.28%) than invaded sites. Overall mean plant canopy cover in cleared sites was significantly higher ($F = 57.58$, $P < 0.001$) than in uninvaded sites.

Overall plant canopy cover did not change during invasion because of equilibrium between increasing *Prosopis* cover and declining grass cover. The decline in grass cover was mainly linked to the loss of the annual grass *Aristida adscensionis* L. and to a much lesser extent of some indeterminate perennial grasses. Only the annual grass *A. adscensionis* ($F = 12.24$, $P = 0.001$; FDR-adjusted $P = 0.016$) and *Prosopis* ($F = 58.09$, $P < 0.001$; FDR-adjusted $P = 0.003$) had significantly different mean canopy covers in uninvaded and invaded sites (Supplementary Table S1). The difference in *Prosopis*

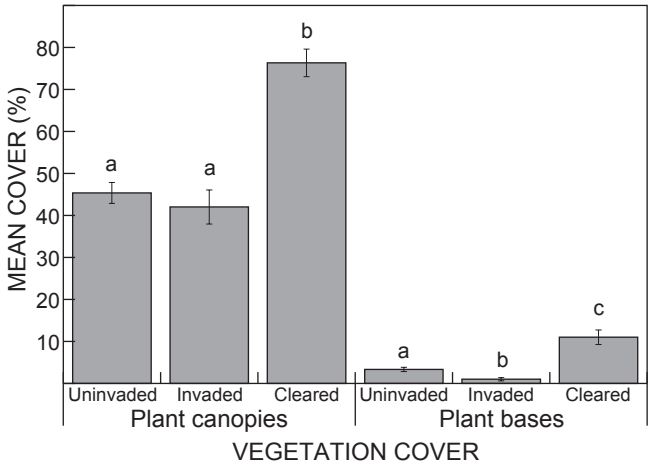

Figure 2: Overall mean plant canopy and basal cover for uninvaded (n = 5), invaded (n = 2) and cleared (n = 3) sites. The error bars represent the standard error. Significance was determined by one-way ANOVA via randomisation

covers between uninvaded and invaded sites (15.12%) was almost the same as the difference in grass canopy cover (13.06%; Supplementary Table S1). Although perennial grasses had significantly (F = 6.00, P = 0.016; FDR-adjusted P = 0.005) different mean canopy covers in uninvaded and invaded sites, there were no significant differences at species level (Supplementary Table S1).

The gain in overall plant canopy cover after clearing was mainly driven by increases in the cover of the annual grass *A. adscensionis* and the perennial grass *Eragrostis obtusa* Munro ex Ficalho & Hiern. Clearing was also accompanied by reductions in the cover of invasive *Prosopis* trees, and to a much lesser extent the succulent shrub *Phyllobolus splendens* (L.) Gerbaulet and the non-succulent shrub *Salsola tuberculata* Fenzl ex Moq. The annual grass *A. adscensionis* (F = 13.53, P = 0.001; FDR-adjusted P = 0.014), perennial grass *E. obtusa* (F = 8.79, P = 0.006; FDR-adjusted P = 0.034), succulent shrub *P. splendens* (F = 5.58, P = 0.030; FDR-adjusted P = 0.021), non-succulent shrub *S. tuberculata* (F = 10.90, P = 0.003; FDR-adjusted P = 0.021) and *Prosopis* (F = 26.87, P < 0.001; FDR-adjusted P = 0.014) had significantly different mean canopy covers in invaded and cleared sites (Supplementary Table S2).

The overall canopy cover in cleared rangeland was higher than the pre-invasion level mainly because of a higher cover of the annual grasses *A. adscensionis* and to a lesser extent the annual grass *S. verticillata*, the perennial grass *E. obtusa* and indeterminate succulent shrubs. Mean canopy cover was significantly different in cleared and uninvaded sites for the annual grasses *A. adscensionis* (F = 12.81, P < 0.001; FDR-adjusted P = 0.006) and *S. verticillata* (F = 6.85, P = 0.008; FDR-adjusted P = 0.031) and the perennial grass *E. obtusa* (F = 28.80, P < 0.001; FDR-adjusted P = 0.006; Supplementary Table S3). Although succulent shrubs had significantly (F = 7.28, P = 0.008; FDR-adjusted P = 0.003) different mean canopy covers in cleared and uninvaded sites, the difference does not occur at species level (Supplementary Table S3).

Effect of invasion and clearing on plant basal cover

Invasion reduced overall plant basal cover from about 3% to 1%, whereas clearing, in turn, increased it to 11% (Figure 2). Cleared rangeland still had 8% more overall plant basal cover than uninvaded rangeland more than four years after clearing (Figure 2). Overall mean plant basal cover in invaded sites (1.00 ± 0.39%) was significantly lower (F = 6.14, P = 0.015) than in uninvaded sites (3.32 ± 0.51%). Cleared sites had significantly higher (F = 16.31, P = 0.010) overall mean plant basal cover (11.00 ± 1.73%) than invaded sites. Overall mean plant basal cover in cleared sites was significantly higher (F = 25.93, P < 0.001) than in uninvaded sites.

The vegetation changes associated with the reduction in overall plant basal cover during invasion were of such small magnitudes that no distinct patterns could be detected at the functional type and species level. There was no significant difference in annual grass (F = 2.74, P = 0.103; FDR-adjusted P = 0.319), perennial grass (F = 2.45, P = 0.182; FDR-adjusted P = 0.319), annual herb (F = 0.30, P = 1.000; FDR-adjusted P = 1.050), succulent shrub (F = 1.28, P = 0.564; FDR-adjusted P = 0.740) and non-succulent shrub (F = 2.05, P = 0.167; FDR-adjusted P = 0.319) mean plant basal cover between uninvaded and invaded sites (Supplementary Table S4).

The increase in overall plant basal cover after clearing was linked to increases in the cover of the annual grass *A. adscensionis* and some indeterminate perennial grasses and non-succulent shrubs. The annual grass *A. adscensionis* (F = 5.10, P = 0.029; FDR-adjusted P = 0.054), perennial grasses (F = 7.08, P = 0.016; FDR-adjusted P = 0.025) and non-succulent shrubs (F = 9.07, P = 0.005; FDR-adjusted P = 0.016) had significantly different mean basal covers in cleared and invaded sites (Supplementary Table S5). Although perennial grasses and non-succulent shrubs had significantly different mean basal covers in cleared and invaded sites, the difference did not occur at species level (Supplementary Table S5).

Overall plant basal cover was higher in cleared than uninvaded rangeland because of higher covers of the annual grass *A. adscensionis* and the non-succulent shrub *Rosenia humilis* (Less.) K.Bremer. The annual grass *A. adscensionis* (F = 8.19, P = 0.005; FDR-adjusted P = 0.038) and the non-succulent shrub *R. humilis* (F = 6.77, P = 0.015; FDR-adjusted P = 0.071) had significantly different mean basal covers in cleared and uninvaded sites (Supplementary Table S6).

Effect of increasing invasion density on plant canopy and basal cover

The relationship between *Prosopis* cover and overall rangeland plant canopy cover conformed to the Type 6 function in SegReg, i.e. an increase in overall rangeland plant canopy cover occurred steeply before a threshold of 6.40% *Prosopis* canopy cover, after which it sharply declined and then increased less steeply (Figure 3). Overall rangeland plant canopy cover declined sharply from 93% to 34% after the threshold (Figure 3).

The relationship between *Prosopis* cover and overall rangeland plant basal cover conformed to the Type 5 function in SegReg (Figure 4). Overall rangeland plant

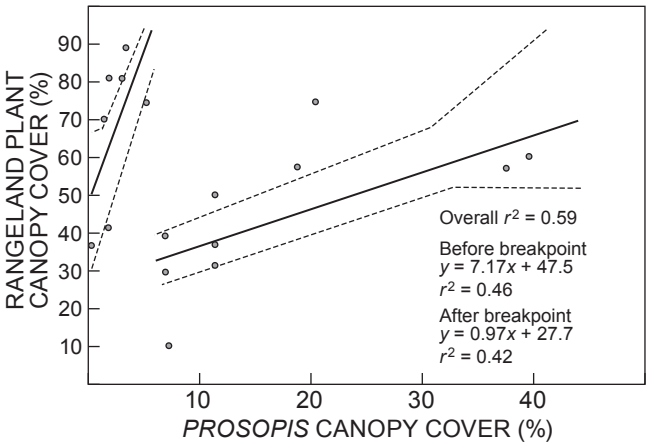

Figure 3: Segmented regression analysis showing the relationship between *Prosopis* cover and overall rangeland plant canopy cover. Also shown are the standard (least-squares) regression equations and 95% confidence intervals

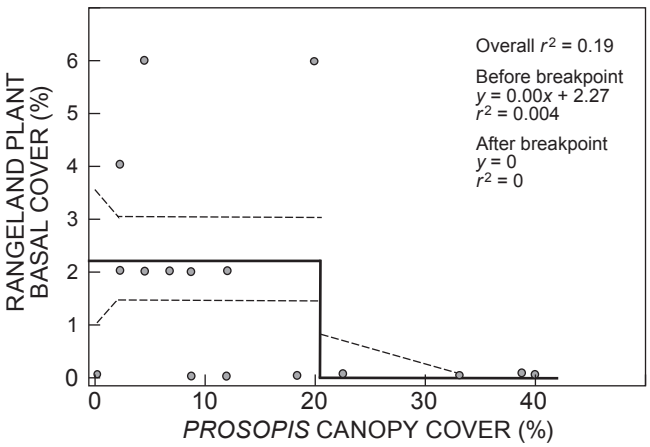

Figure 4: Segmented regression analysis showing the relationship between *Prosopis* cover and overall rangeland plant basal cover. Also shown are the standard (least-squares) regression equations and 95% confidence intervals

basal cover did not change during invasion up to a threshold of 20.40% *Prosopis* canopy cover, after which it fell sharply from 2.27% to 0% (Figure 4).

Discussion

Prosopis trees have been documented to reduce grass abundance in their understory and neighbourhood (McDaniel et al. 1982; McClaran and Angell 2006; Simmons et al. 2008). As a result, we expected changes in overall rangeland plant canopy and basal cover during invasion and clearing at our study site to be mainly driven by changes in grass cover, with invasion reducing overall plant canopy and basal cover and clearing restoring the cover to pre-invasion levels. Our results confirmed most of the expectations except that invasion did not result in a decrease in overall canopy cover and clearing did not restore overall canopy and basal cover to pre-invasion levels. Instead, increasing *Prosopis* canopy cover during invasion compensated for lost grass canopy cover and kept overall plant canopy cover constant, while clearing increased overall plant canopy and basal cover to extents far above pre-invasion levels.

Apart from *Prosopis* cover changes, overall plant canopy and basal cover changes during invasion and clearing at our study site were mainly driven by changes in the cover of the annual grass *A. adscensionis*. This grass, which dominated our heavily grazed study site likely because it is resilient to overgrazing (Esler et al. 2006), is shade-intolerant and a poor interspecific competitor for moisture and nutrients (Varshney 1968). Invading *Prosopis* trees extract soil moisture and nutrients from far beyond their crown areas through extensive lateral root systems (Tiedeman and Klemmedson 1973) and most likely reduced *A. adscensionis* cover in the neighbouring open areas by competing with the grass for moisture and nutrients. The balance between increased *Prosopis* canopy cover and lost *A. adscensionis* cover appears to have been a serendipitous outcome that does not occur at *Prosopis* covers higher or lower than those at our study site (i.e. greater or lesser than 15% *Prosopis* cover; see discussion on threshold effect of *Prosopis* invasion below). The increase in overall canopy and basal cover after clearing to levels surpassing pre-invasion conditions probably resulted from elevated soil fertility in cleared rangeland. *Prosopis* trees fix nitrogen and accumulate soil nutrients such as magnesium, potassium and phosphorous under their canopies (Tiedeman and Klemmedson 1973; Barth and Klemmedson 1982; Gadzia and Ludwig 1983; Klemmedson and Tiedeman 1986; Frias-Hernandez et al. 1999; Geesing et al. 2000; Reyes-Reyes et al. 2002). As a result cleared rangeland at our study site could have been more fertile than uninvaded rangeland and consequently supported greater grass production and cover. The enhanced post-invasion soil fertility and its effects are, however, most likely temporary as they are a legacy of ecological processes (i.e. *Prosopis* nitrogen fixation and soil nutrient accumulation) that are no longer operational (see Klemmedson and Tiedeman 1986).

Grasses usually contribute the most to overall canopy and basal cover in semi-arid rangelands (Herrick et al. 2005a). Invading *Prosopis* trees have a threshold effect on rangeland grass production where they do not seem to have any significant effect until their cover surpasses certain thresholds (McDaniel et al. 1982; Warren et al. 1996). This phenomenon probably explains the complex threshold effects that characterised relationships between *Prosopis* cover and overall plant canopy and basal cover at our study site. The steep rise in overall plant canopy cover during early stages of invasion (below the 6% *Prosopis* cover threshold) was probably caused by the incorporation of invading *Prosopis* tree cover into overall rangeland canopy cover without any loss to indigenous grass cover. However, once *Prosopis* cover exceeded the 6% cover threshold and invasive trees began to suppress neighbouring indigenous grasses, overall rangeland canopy cover declined sharply. The less rapid increase in overall canopy cover that occurred after the threshold was solely linked to increasing *Prosopis* tree cover. The same process probably occurred

with overall basal cover, which remained constant up to a threshold of 20% *Prosopis* cover, after which it collapsed as invading *Prosopis* trees began to reduce understory and neighbouring grass cover. The dynamic interactions between invading *Prosopis* trees and *A. adscensionis* at our study site appear similar to those reported between encroaching savanna woody trees and their natural herbaceous undergrowth (see review in Introduction).

Our data imply that at low cover invasive *Prosopis* trees reduce rangeland erosion potential by augmenting indigenous vegetation cover. Vegetation cover promotes rainfall infiltration and reduces runoff (see references in Introduction). However, above a certain threshold cover (6% at our study site), *Prosopis* trees begin to increase rangeland erosion potential by reducing indigenous vegetation cover. The threshold effect is sudden and results in a drastic decline in indigenous vegetation cover. Although *Prosopis* trees continue to contribute to overall rangeland vegetation cover after the threshold collapse of indigenous vegetation cover, their effect on rangeland erosion potential is probably limited at this stage. Rainwater dripping from tree canopies onto exposed soil surfaces can dislodge soil as effectively as rain directly striking the soil (Herrick et al. 2005b). In addition, the collapse of indigenous plant basal cover after the threshold is exceeded likely results in the absence of physical obstructions to dissipate the erosive capacity of runoff.

It is not always possible to completely clear *Prosopis* trees from invaded areas. *Prosopis* clearing is expensive and in the Nama-Karoo costs often exceed the value of rangeland (Zimmermann and Pasiecznik 2005). As a result, completely removing *Prosopis* trees from invaded areas (farms, watersheds, etc.) is usually financially difficult or economically unfeasible. In addition, some landowners (a small minority; Shackleton et al. 2015a) are opposed to completely clearing *Prosopis* from their properties as they perceive the trees to be beneficial. In such situations, the threshold effect of *Prosopis* impact (Ndhlovu et al. 2011; this study) may be of great use in managing invasions. For example, critical areas to be cleared can be identified and prioritised based on threshold cover to maximise benefit from limited control efforts. In areas where invasions are dense, but complete removal of trees is undesired or impossible, judicious tree thinning (see Smit and Rethman 1999; Smit 2003, 2004, 2005) based on threshold cover can be applied to harness positive effects of low-density *Prosopis* trees.

We, however, caution against application of these management practices unless complete clearance of *Prosopis* is absolutely impossible or undesirable. *Prosopis* trees have an immense capacity for reinvasion in the absence of natural enemies such as seed-feeding insects and fungal pathogens. The trees can produce 9–20 t ha^{-1} of pods annually (March et al. 1996). The pods are highly palatable to livestock, which spread seed widely across the landscape (March et al. 1996). Widespread reinvasion can occur without warning as *Prosopis* germination occurs as 'bursts' in response to highly favourable but irregular climatic events, such as periods of exceptional rainfall and floods (March et al. 1996). Introducing seed-feeding insects (Zimmermann 1991; Moran et al. 1993; Roberts 2006; Zachariades et al. 2011) may ameliorate the risk of widespread reinvasion when complete clearing of *Prosopis* trees is impossible or undesirable. However, the efficacy of biological control agents in current use for *Prosopis* in South Africa (i.e. the seed-eating beetles *Algarobius prosopis* J.L. LeConte, 1858, *A. bottimeri* Kingsolver, 1972 and *Neltumius arizonensis* Schaeffer, 1904) is uncertain (Shackleton et al. 2014). Until more efficacious biocontrol agents become available (see Zachariades et al. 2011; Shackleton et al. 2014) management efforts should aim, whenever possible, to completely clear *Prosopis* from invaded areas.

Conclusion

Our study suggests that, at low cover, *Prosopis* trees contribute positively to overall rangeland vegetation cover. However, once *Prosopis* cover exceeds a critical threshold, the trees begin to affect overall vegetation cover negatively. Below critical threshold cover levels, *Prosopis* trees do not negatively affect indigenous vegetation cover and add to overall rangeland cover. Above critical threshold cover levels, *Prosopis* trees drastically reduce the cover of indigenous herbaceous plants (especially grasses) lowering overall rangeland cover. Overall vegetation cover recovers after *Prosopis* clearing, being temporarily higher than pre-invasion levels because of enhanced post-invasion soil fertility. *Prosopis* trees fix nitrogen and accumulate various soil nutrients under their canopies, which persist as a transient legacy after clearing. *Prosopis*–vegetation cover relations have implications for erosion potential in invaded rangelands. Our findings suggest that *Prosopis* trees reduce rangeland erosion potential at low cover and increase it after they exceed a critical threshold cover. Information about the thresholds of *Prosopis* impact can be of great management value. For example, it can be used to direct clearing efforts for maximum benefit when resources are limited.

Comparative observational studies are useful, but do not provide direct evidence of cause and effect. There is need for controlled experimental studies to verify the validity of our findings. An example is the unpublished study by Saayman and Botha (2007) near our site (see Ndhlovu 2011). More studies are also needed to verify if our findings apply consistently across the biome. One way to achieve this is by replicating our study across the range of environmental and management (e.g. rainfall, stocking level and invasion density) conditions occurring in the Nama-Karoo. Such validatory studies are crucial for accurately extrapolating *Prosopis* impact over large spatial areas, and for informing biome-scale management strategies.

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